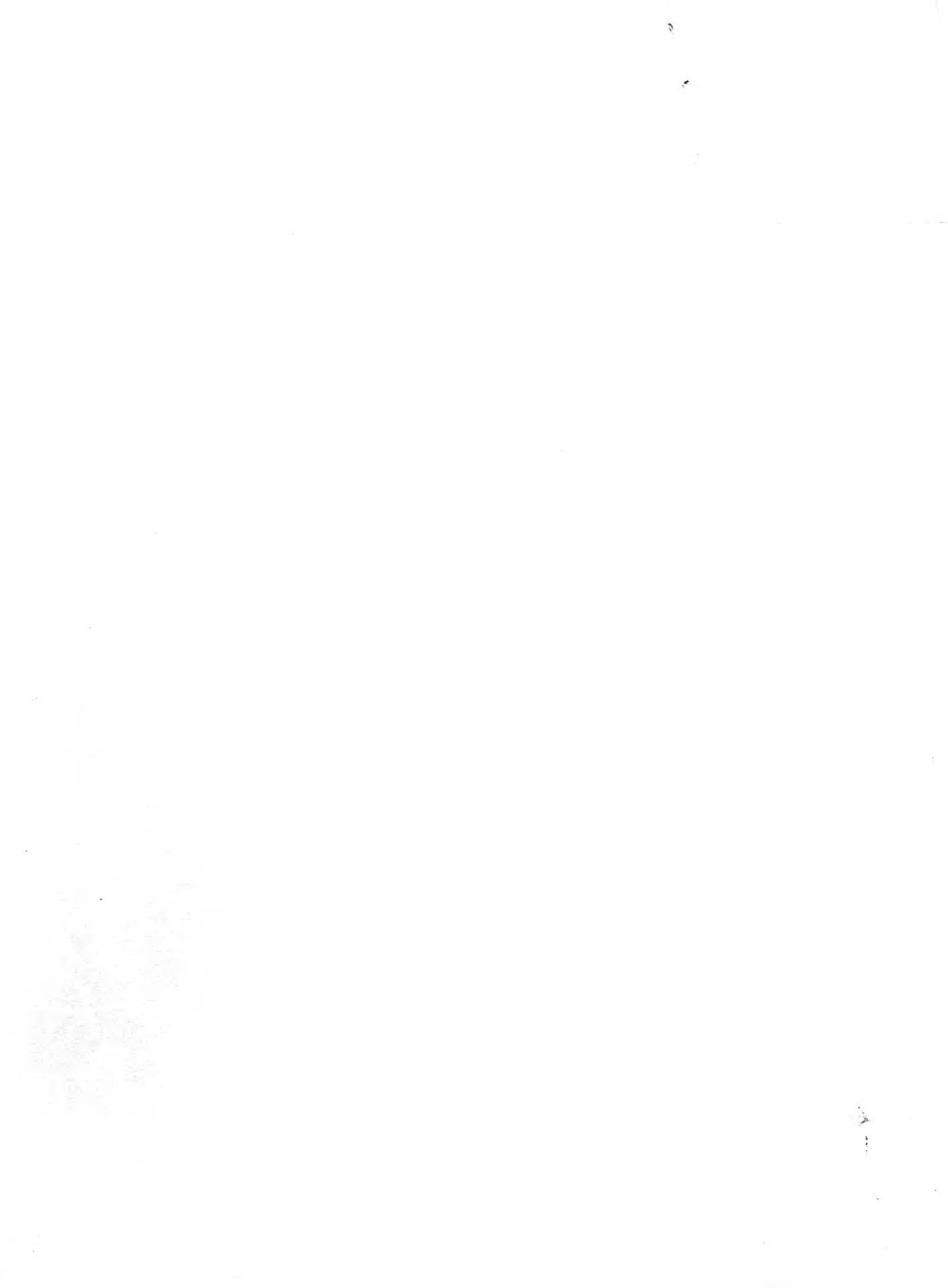


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Adaptive Variation and Seed Transfer for Ponderosa Pine in Central Idaho

G. E. Rehfeldt¹

ABSTRACT

When planted and compared in the same environments, populations from elevationally or geographically mild sites demonstrated the most growth, mainly because of the long duration and rapid rate of shoot elongation. Populations from relatively cold sites were comparatively shorter largely because growth ceased early. Populations from the South Fork of the Salmon River, however, combined a high rate of shoot elongation with a short duration of growth and thereby were capable of high productivity while maintaining adaptability for severe sites. In artificial reforestation, seed transfer from most populations should be limited to ± 650 feet of the elevation at the source. Tests should be established to determine if South Fork populations can be moved beyond the recommended limits in an attempt to increase productivity on harsh, cold sites.

KEYWORDS: *Pinus ponderosa*, seed zones, reforestation, forest genetics, ecological adaptation

Plant populations that occupy contrasting environments commonly differ genetically for numerous traits that convey environmental adaptation. In forest trees, physiological attunement to the environment is commonly displayed in traits that comprise an annual sequence of developmental events. This sequence begins with bud burst in the spring; includes shoot expansion, leaf maturation, cambial enlargement, bud development, and lignification; and concludes with cold acclimation in the fall. For populations to be adapted, the entire sequence must be completed within the growing season, a period terminated by frost but often interrupted by drought. Adaptive differentiation thus results from physiologic attunement of the entire sequence of developmental events to a growing season whose length varies considerably among sites and years. Consequently, the timing of individual events within the developmental cycle tend to be intercorrelated.

When Rocky Mountain populations of ponderosa pine are grown in common environments, populations from mild environments exhibit a long duration and late cessation of shoot elongation; a long length and late maturation of leaves; a late date for completion of lignification; and a tall stature associated with a high growth potential (innate capacity for growth). A late cessation of development, however, conveys a high susceptibility to fall frosts, and a high growth potential reflects susceptibility to snow damage. By contrast, populations adapted to short growing seasons cease development early, display a low growth potential, but are most tolerant of early fall frosts and heavy snows (Madsen and Blake 1977; Rehfeldt 1979b, 1980, 1986a, 1986b).

Because genetic differentiation occurs along environmental gradients, genetic variation is clinal (continuous) and can be described as systematic patterns of variation across geographic and elevational gradients. The clines, therefore, are basic to the development of seed transfer guidelines, the environmental limits to which seeds can be transferred from their origin before maladaptations begin reducing the productivity of artificial reforestation.

This paper is the second in a series devoted to describing genetic variation among populations of ponderosa pine in central Idaho. The first paper (Rehfeldt 1986a) detailed experimental methods and statistical procedures and applied general results to concepts of adaptive variation. The present paper refines statistical procedures to describe adaptive clines and develop seed transfer guidelines specifically for the Salmon River Mountains.

METHODS

Population differentiation was studied in seedlings from 64 populations (appendix) that sampled the ecologic, geographic, and elevational distribution within which the species is of commercial importance in central Idaho (fig. 1). As detailed previously (Rehfeldt 1986a), cones were collected in a manner to adequately sample genetic diversity, and seedlings were compared in separate studies of (1) growth and development in the field, (2) the periodicity of shoot elongation in the greenhouse, and (3) freezing tolerance in the laboratory.

¹Plant geneticist located at Intermountain Station's Forestry Sciences Laboratory, Moscow, ID.

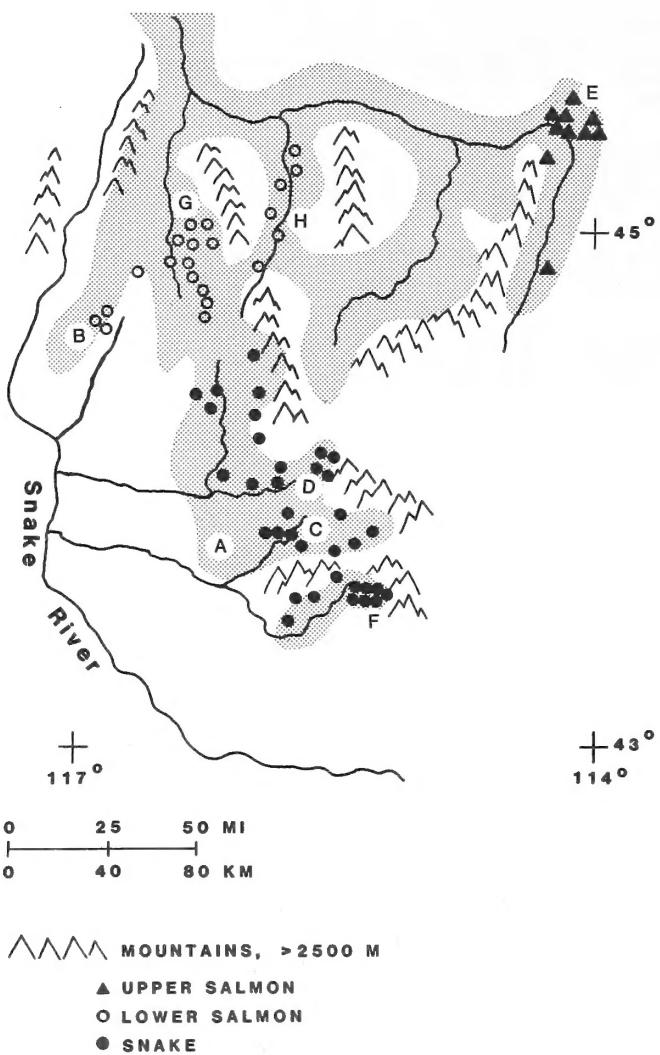


Figure 1—Geographic distribution of ponderosa pine (shading) and location of sampled populations. Letters A to G locate the elevational clines presented in figure 2.

Twelve variables originally were used to assess genetic variation for several events within the annual sequence. Because events within the sequence are intercorrelated, a relatively small number of variables can be used as keys to describing genetic variation within the entire sequence. In this paper, 3-year height and the rate and duration of shoot elongation are used to reassess patterns of genetic variation according to models that are developed for practical application.

Selection of a regression model that best described patterns of genetic variation required screening several models of the general form:

$$Y_{ij} = b + \sum_j \beta X_{ij} + \sum_j \gamma X_{ij}^2$$

where Y_{ij} is one of three dependent variables for population i in subregion j (fig. 1); X 's are independent variables describing the origin of population i , and b , β , and γ are regression coefficients.

Because the objectives of the regression analyses were to detect and describe patterns of genetic variation, a

large number of independent variables were screened for association with the dependent variables. Independent variables included elevation, latitude, longitude, northwest departure, southwest departure, arcs of a circle centered at 44° latitude and 114° longitude, and the squares of all variables. Northwest and southwest departures were obtained by rotating the grid of longitude and latitude by 45°. The five geographic variables were also nested within three geographic subregions (fig. 1). Thus, 32 independent variables were screened by stepwise regressions for maximizing R^2 (SAS 1982). The best fitting regression model was selected according to the following criteria (Draper and Smith 1981): statistical significance, smallest residual variance, no relationship between residuals and independent variables, and no evidence of overfitting—the fitting of a model to individual samples rather than to the group as a whole.

RESULTS AND DISCUSSION

The best fitting regression models were all statistically significant ($p < 0.01$) and accounted for 67 percent of the variance among populations in 3-year height, 48 percent for the rate of shoot elongation, and 68 percent for the duration of shoot elongation. The models included 14 to 18 independent variables and thereby could reflect overfitting. Consequently the practical significance of a model is interpreted according to the least significant difference (Steel and Torrie 1960) among populations at the 80 percent level of probability ($lsd 0.2$). A relatively low level of probability is used to guard against accepting no differences among populations when differences actually exist.

Patterns of genetic variation described by the models can be presented as elevational clines for several geographic localities (figs. 2 and 3) or by geographic clines for a constant elevation (figs. 4 and 5). In figures 2 and 3, the elevational clines are presented for eight localities whose geographic position is keyed to figure 1:

Symbol	Locality
A	Lower Boise River
B	Council
C	Idaho City
D	Lowman
E	North Fork
F	Featherville
G	New Meadows
H	South Fork

The elevational clines (figs. 2 and 3) show that populations from the rather mild environments at low elevation tend to be tall because of a long duration of shoot elongation. Populations from high elevations, where frost-free periods are short, have a short duration of elongation and a low growth potential. The slope of these clines implies that at any locality, populations separated by about 1,300 feet differ by an amount equal to $lsd 0.2$. Thus, such populations differ genetically with a probability of about 80 percent.

The elevational clines also illustrate that populations of similar genetic constitution recur at different elevations across the landscape. Populations of a moderate duration,

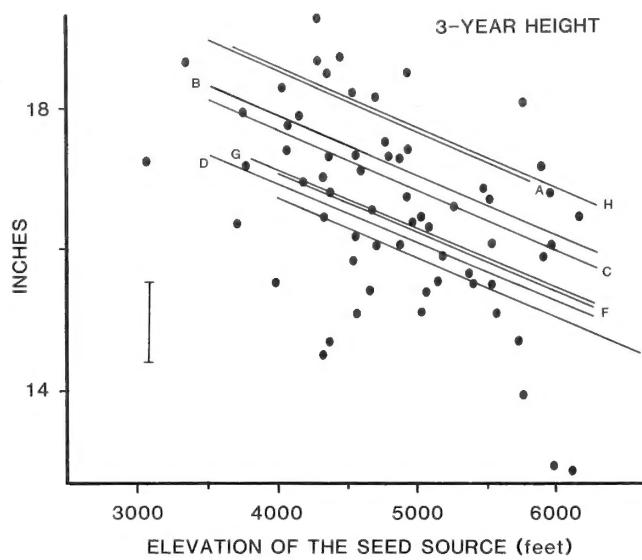


Figure 2—Elevational clines for the 3-year height of seedlings from eight geographic locations keyed to figure 1. Brackets quantify l_{sd} 0.2.

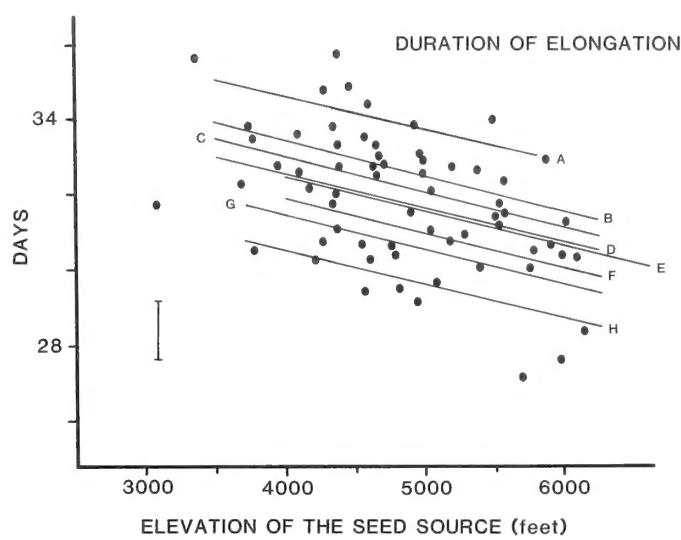


Figure 3—Elevational clines for the duration of shoot elongation of seedlings from eight geographic localities keyed to figure 1. Brackets quantify l_{sd} 0.2.

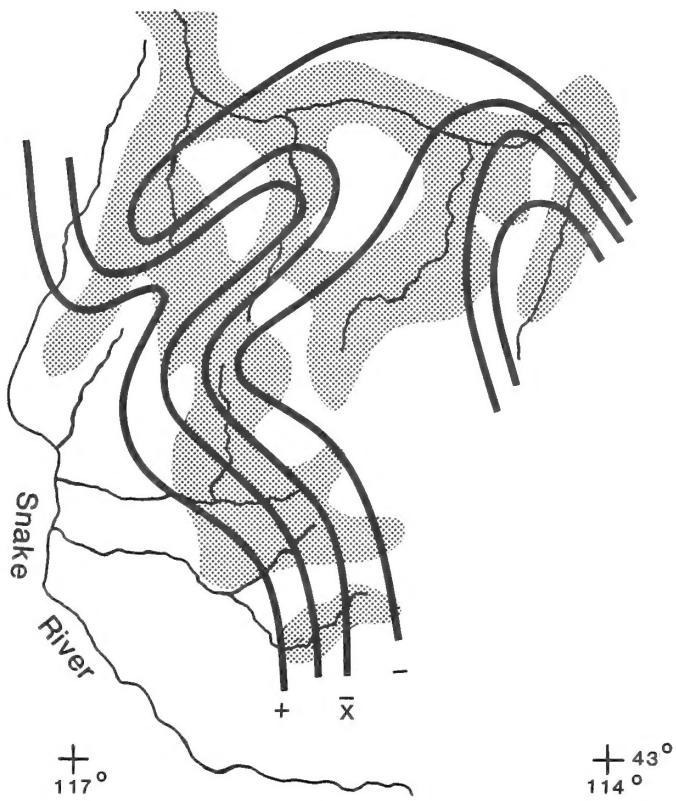


Figure 4—Geographic patterns of variation for 3-year height described by isopleths (contour lines) of equal performance at the mean elevation (3,500 feet). The interval between isopleths equals $1/2[l_{sd}(0.2)]$. Isopleths represent positive or negative deviations from the mean value (\bar{x}) of all populations.

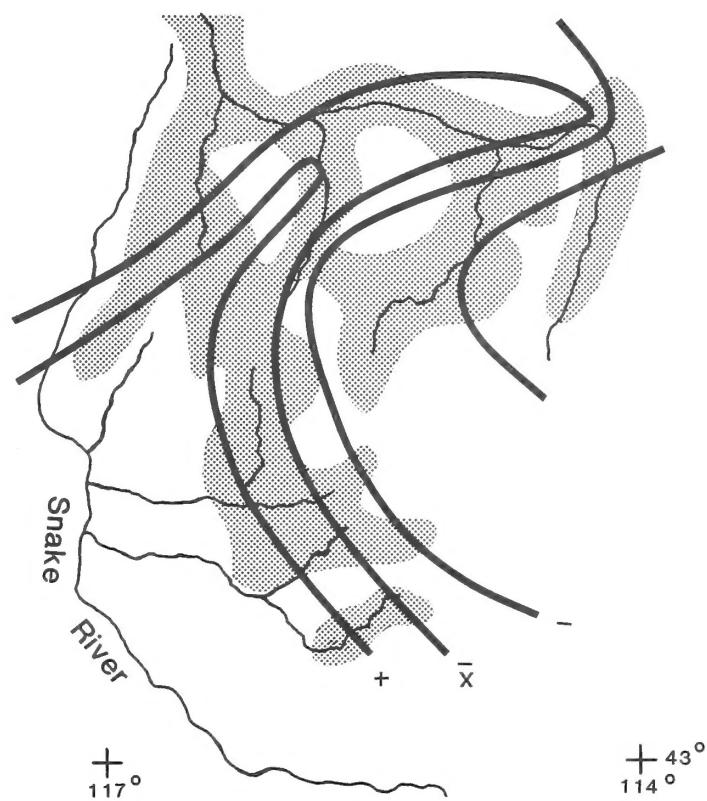


Figure 5—Geographic patterns of variation for rate of shoot elongation described by isopleths (contour lines) of equal performance at the mean elevation (3,500 feet). The interval between isopleths equals $1/2[l_{sd}(0.2)]$. Isopleths represent positive or negative deviations from the mean value (\bar{x}) of all populations.

33 days for example (fig. 3), would be expected to occur at 3,500 feet at Lowman, 4,000 feet at Idaho City, and 5,000 feet at Council. This also means that populations growing at the same elevation in different geographic localities can be different genetically. Of all populations from an elevation of 5,000 feet, for example, those from the South Fork and Lower Boise River have the greatest growth potentials while those from the North Fork have the lowest. Recurrence of similar genotypes is dependent on the recurrence of environments with similar growing season, the environmental factor primarily responsible for adaptive differentiation. Consequently, populations of similar adaptive norms are distributed across the landscape in patterns that are oblique to elevation.

Geographic patterns of genetic variation are detailed in figures 4 and 5 for 3-year height and the rate of shoot elongation, respectively. In these figures, the distance between isopleths (contour lines) equals $\frac{1}{2}lsd(0.2)$. This means that localities separated by the distance between two isopleths support populations that are genetically different, with a probability of about 80 percent. According to figure 4, populations of greatest growth potential occur in those environments at relatively low elevations that are adjacent to the steppe, exactly where ponderosa pine is ecologically dominant (Steele and others 1981). Toward the north, northeast, and east, the climate is strongly influenced by particularly massive mountains. As a result, growth potentials decline as the frost-free period declines. Figure 5 depicts a similar pattern for the rate of shoot elongation: populations of highest growth potential also tend to have the fastest rates of elongation.

These figures together show that populations with the highest growth potential tend to originate from the mildest environments and achieve a high potential by means of a long duration and rapid rate of shoot elongation. A notable exception to this generality involves populations from the South Fork where a mild growing season is commonly truncated by drought. These populations express a high growth potential (fig. 3) that is achieved by means of a high rate of shoot elongation (fig. 5) despite having the shortest duration of elongation (fig. 2) of any populations tested. South Fork populations, therefore, express a growth potential that is typical of populations from mild environments while maintaining a short duration of elongation, which is typical of populations adapted to cold sites. Superior performance of families from the South Fork was also evident after 16 years of field testing at four locations (Rehfeldt 1980).

PRACTICAL APPLICATION

Systematic patterns of genetic variation have developed from the action of natural selection in synchronizing developmental events with the local climate. Consequently, the patterns are directly applicable to artificial reforestation. Planted trees must be adapted to the planting site if productivity is to be maximal. Adaptation is secured by limiting the distance that seeds are transferred from their origin. Consequently, limits to seed transfer must reflect geographic and elevational patterns of variation.

One way of controlling maladaptation is to construct discrete seed zones, the boundaries of which are determined by the smallest geographic and elevational intervals across which differentiation can be detected (Rehfeldt 1979a). Differentiation along the elevational cline (figs. 2 and 3) suggests that a seed zone for ponderosa pine should not encompass more than 1,300 feet of elevation. This means that seed from a single source should not be transferred more than ± 650 feet elevationally. In addition, the geographic clines of figure 4 describe seed zones that should not encompass more than two of the geographic bands between isopleths. Thus, approximately three geographic zones would be suitable for the region, and seeds from a single source should not be transferred a distance equivalent to more than ± 1 band. These elevational and geographic restrictions jointly delineate six seed zones for the ponderosa pine forests of central Idaho.

Discrete seed zones, however, compartmentalize continuous genetic variation and, thereby, tend to be inflexible, inefficient, and uneconomical. An alternative procedure involves constructing floating transfer guidelines that are based on the recurrence of similar genotypes at different elevations in geographically separated localities. According to floating guidelines, seed can be transferred across isopleths (fig. 4), but each time seed is transferred across a geographic interval equaling the interval between isopleths, the elevations at which the seed is to be used should be adjusted. When transferring across isopleths of high to low value, the interval should be adjusted downward by 650 feet; when transferring from lower to higher value, the interval should be adjusted upward by 650 feet.

Two examples:

1. Assume that seed originates from 5,000 feet anywhere along the isopleth representing the mean of all populations (fig. 4). This seed should be used between 4,350 and 5,650 feet in lands adjacent to the contour. In transferring the seed across one isopleth of larger value, the seed should be used between 5,000 and 6,300 feet. In transferring the seed across an isopleth of lesser value, the seed should be used between 3,700 and 5,000 feet. And transfers across two contours of lesser value should be used between 3,050 and 4,350 feet.

2. By recognizing that the guidelines are based on equivalent performance, floating transfer guides can be constructed from the elevational clines of figure 2. Thus, seed collected from 5,000 feet at Idaho City (locality C) can be used at $4,100 \pm 650$ feet at Lowman (D), at $4,440 \pm 650$ feet at New Meadows (G), at $5,200 \pm 650$ feet at Council (B), and at $6,000 \pm 650$ feet in the South Fork (H). In these ways, seed from a single source or seed orchard can serve a much broader geographic area than under the concept of discrete seed zones.

Populations from the South Fork may offer unique possibilities to forest management. These populations express a growth potential that is typical of populations adapted to mild environments while maintaining an adaptedness that is typical of populations adapted to severe environments. This suggests that in severe environments productivity might be increased by importing

foreign populations. But additional research and operational assessments must be completed before general guidelines can be developed for using these seeds.

These recommendations for limiting seed transfer evolved from statistical models based on the performance of young trees under controlled conditions. On the one hand, the environmental events responsible for the systematic patterns may occur so infrequently that managers might risk transferring fast-growing populations into severe environments in an attempt to increase productivity. Indeed, genetic differentiation may have been detected at levels associated with productive differences so small as to be immaterial. But, on the other hand, small adaptive differences observed at young ages may accumulate and thereby portend large differences in the future. As Dietrichson (1964) has shown, many of these accumulated effects involve insects and diseases. Consequently, the models need practical verification. Verification can come only from planting programs that not only incorporate these guidelines but also maintain precise records on the exact location from which planted trees originated. Productivity of such plantings will test the applicability of these guidelines.

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APPENDIX: LOCATION AND PERFORMANCE OF POPULATIONS

Collection number	Location	Latitude	Longitude	Elevation	Height	Duration	Rate
		- - - - Degrees - - - -		Meters		cm	
1	Panther Creek	44.95	114.33	1829	32.4	27.46	2.74
2	Sheep Creek	45.50	113.92	1341	36.3	33.66	4.34
3	Bald Mountain	45.50	114.17	1875	32.3	30.32	3.45
4	Squaw Creek	45.50	114.22	1743	36.7	26.93	3.64
5	Papoose Creek	45.45	114.22	1646	38.7	32.40	3.95
6	Lower Papoose	45.42	114.18	1426	45.4	32.49	3.56
7	Warm Spring Ridge	43.85	115.88	1433	40.1	32.88	3.75
8	Sagehen	44.32	116.23	1585	39.5	32.70	3.86
9	Third Fork	44.37	116.33	1158	43.0	30.52	3.63
10	Powelson Creek	44.78	115.87	1829	39.9	30.35	3.48
11	Bear Creek	43.95	115.47	1829	38.1	30.17	3.40
12	South Fork of Payette	44.07	115.50	1280	44.7	30.18	4.10
13	Mill Creek	44.67	116.87	1250	43.4	33.81	4.04
14	Rabbit Creek	43.80	115.72	1829	41.9	31.15	4.04
15	Mud Creek	45.05	116.38	1341	43.3	31.99	4.16
16	Rough Creek	44.90	116.48	1128	40.8	32.15	3.98
17	Circle Creek	45.05	116.27	1280	42.4	32.25	3.79
18	Three Mile	44.98	116.22	1341	46.1	31.85	3.78
19	Dutch Creek B	43.73	115.45	1676	41.7	31.19	3.79
20	Trail Creek	43.60	115.75	1341	48.1	35.83	4.13
21	West Fork Creek	44.30	115.87	1219	38.5	32.83	4.11
22	Garden Valley	44.07	115.93	945	42.9	31.66	3.75
23	Dutch Creek A	43.80	115.37	1402	39.6	30.25	3.86
24	Camp Creek	44.88	115.70	1311	46.6	30.75	3.78
25	Zena Creek	45.68	115.75	1463	43.3	29.58	4.20
26	Wagon Town A	43.62	115.28	1768	34.7	30.12	3.48
27	Wagon Town B	43.62	115.18	1707	38.5	31.45	3.79
28	Wagon Town C	43.62	115.72	1798	42.5	32.72	3.57
29	Elk Creek	43.62	115.72	1311	46.6	34.67	3.61
30	Long Gulch	43.62	115.62	1463	43.6	30.46	3.98
31	Bear Run	43.83	115.83	1341	42.7	33.75	3.47
32	Humbug	43.83	115.72	1250	44.2	32.54	3.79
33	Clay Creek SPA	43.95	115.83	1341	40.8	33.21	3.93
34	Dutch Creek II	43.83	115.28	1341	36.7	30.98	3.60
35	Weatherby Flats	43.83	115.28	1402	45.1	34.20	3.69
36	Canyon Creek	44.22	115.18	1554	38.7	30.99	4.08
37	Ten Mile Creek	44.12	115.28	1341	41.8	32.70	3.76
38	Logging Gulch	44.12	115.62	1250	45.6	32.62	3.96
39	Dry Buck	44.12	116.17	1524	43.4	32.99	4.40
40	Second Fork of Squaw Creek	44.37	116.17	1402	42.7	33.50	3.92
41	Wash Creek	44.05	115.83	1158	44.6	33.53	3.79
42	Bell Creek	44.22	115.83	1036	46.5	35.78	3.65
43	Carpenter Creek	44.12	115.83	1494	40.0	31.43	4.30
44	Crawford Creek II	44.53	115.95	1554	37.6	31.89	3.71
45	Skunk Creek	44.37	115.95	1585	38.6	30.67	3.34
46	Crooked River SPA ¹	44.83	116.67	1402	40.4	30.87	3.07
47	Calamity SPA	44.70	116.67	1768	45.1	30.40	3.97
48	Bear Gulch	44.97	116.42	1646	38.9	29.93	3.93
49	Slaughter Gulch	44.97	116.42	1554	40.5	29.72	3.98
50	Shingle Flat	44.80	116.28	1433	41.3	33.26	3.73
51	Mill Creek Basin	44.70	116.28	1524	46.2	33.84	4.13
52	Tamarack Creek	44.62	116.80	1372	46.5	34.71	4.42
54	Pony Creek	45.25	115.62	1859	40.9	28.22	3.77
55	Barker Gulch II	43.17	115.18	1433	38.2	32.82	3.87
56	Abbot Gulch	43.17	115.18	1402	37.7	29.47	3.11
57	Pine Gulch	43.17	115.18	1524	43.3	30.34	3.65
58	Gardner Gulch	43.17	115.00	1524	41.5	29.37	3.97
59	Grouse Gulch SPA	43.50	113.92	1524	40.9	32.62	3.43
60	Lost Creek	44.83	116.42	1158	42.9	33.75	3.90
61	Frog Pond	44.80	116.28	1067	41.2	30.91	4.02
62	Burnt Basin	44.62	116.17	1615	41.9	33.68	3.76
63	Hot Springs Creek	45.32	114.33	1707	37.6	32.13	4.02
64	Vine Creek	45.63	114.00	1707	39.8	31.70	3.67
65	Silverleads	45.45	113.97	1798	39.6	30.83	3.82

¹Seed production area.

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Intermountain Research Station
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